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Decline of Zooplankton Populations Following Eutrophication of Lake 227, Experimental Lakes Area, Ontario: 1969-1974

D.F. Malley, P.S.S. Chang, and D.W. Schindler

Central and Arctic Region
Department of Fisheries and Oceans
Winnipeg, Manitoba R3T 2N6

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ABSTRACT

Weekly additions of N and P to oligotrophic Lake 227 in the Experimental Lakes Area, northwestern Ontario, during the ice-free seasons of 1969 to 1974 caused marked increases in standing algal biomass and primary production. Despite this, planktonic crustaceans and rotifers declined in biomass and species diversity with fertilization. Crustacean biomass reached low levels by July 1972 and remained low throughout 1973, recovering somewhat in 1974. Cladocerans and calanoid copepods declined in numbers more severely than cyclopoid copepods. Rotifers increased in total numbers and biomass in 1970 and 1971. Thereafter numbers and biomass declined to levels in 1974 below those at the start of fertilization. The decline in zooplankton biomass in 1970 to 1972 is attributed to a combination of high pH in the epilimnion, reaching 10.0 on occasion, and anoxic areas in the metalimnion and hypolimnion. There is no evidence that the zooplankton were food-limited and it is unlikely that predation by fish, Chaoborus or predaceous zooplankton accounted for the severe declines in crustacean populations. On the other hand, in 1974, circumstantial evidence suggests that Chaoborus reached high numbers. Chaoborus is suggested to be responsible for the decline in rotifers and for the low copepod abundance in this year.

Key words: whole-lake; experimental fertilization; Calanoida; Cyclopoida; Cladocera; Rotifera; pH; O_2; predation; Chaoborus; minnows.

RÉSUMÉ

Malley, D.F., P.S.S. Chang, and D.W. Schindler. 1988. Decline of zooplankton populations following eutrophication of Lake 227, Experimental Lakes Area, Ontario: 1969-1974. Can. Tech. Rep. Fish. Aquat. Sci. 1619: iv + 25 p.

L'addition hebdomadaire de N et de P dans le lac oligotrophe 227 de la Région des Lacs Expérimentaux du nord-ouest de l'Ontario, de 1969 à 1974 pendant la saison des eaux libres, a provoqué une augmentation pronouncée de la biomasse algale sur pied et de la production primaire. Malgré cette augmentation, la biomasse et la diversité des espèces de crustacés et de rotifères planctoniques a diminué avec la fertilisation. En juillet 1972, la biomasse de crustacés est descendue à un faible niveau, c'est maintenue à ce niveau pendant toute l'année 1973 pour ensuite remonter légèrement en 1974. Le populations de cladocères et de copépodes Calanoïdes ont diminué de manière plus marquée que celles des copépodes Cyclopoïdes. Le nombre total et la biomasse des rotifères ont augmenté en 1970 et 1971, puis ont diminuë pour atteindre, en 1974, un niveau inférieur à celui qu'on observait avant le début de la fertilisation. Le déclin de la biomasse zooplanctonique de 1970 à 1972 est attribuée à la combinaision d'un pH élevé dand l'épilimnion (jusqu'à 10,0 à l'occasion) et de zones anoxiques dans le métalimnion et l'hypolimnion. Rien n'indique que la nourriture ait constitué un facteur limitant de la croissance Chaoborus ou par le organismes zooplanctoniques prédateurs soit à l'origine de la forte baisse des populations dede crustacés. Par contre, des données accessoires semblent indiquer qu'en 1974, la population de Chaoborus a atteint un niveau élevé, ce qui laisse entendre que les Chaoborus seraient responsables du déclin des rotifères et de la faible abondance de copépodes pendant cette année.

Mots-clés: lac entier; fertilisation expérimentale; Calanoïdes; Cyclopoïdes; cladocères; rotifères; pH; oxygène; prédation; Chaoborus; cyprinidés.

INTRODUCTION

Zooplankton have generally been found to respond to the eutrophication of lakes in two ways. In some cases, the standing biomass of herbivorous zooplankton has increased in response to fertilization (Smith 1969; LeBrasseur and Kennedy 1972; Patalas and Salki 1973), although the observed increases are often considerably less than the increase seen in the standing crop of phytoplankton (Brooks 1969; de Infante 1978; Hakkari 1978). When lakes of different trophy were compared, the more eutrophic lake exhibited higher production and biomass of zooplankton than the less eutrophic one (Hilbricht-Ilkowska and Weglenska 1970).

In other cases, although eutrophication stimulated phytoplankton biomass, it caused no increase in that of zooplankton. Seven additions of fertilizer to Bare Lake, Alaska over a four-year period increased primary production and standing algal biomass but caused no general increase in abundance of zooplankton (Nelson and Edmondson 1955). Little overall difference in zooplankton biomass was found between two basins of a double-basined lake in northwestern Ontario even though phytoplankton primary production and standing biomass were markedly increased in one basin over the other in response to the fertilization (Malley 1977).

Malley and Chang (1980) reported a third distinct response of zooplankton to eutrophication. In Lake 227 in the Experimental Lakes Area of northwestern Ontario, zooplankton declined in total biomass following fertilization. This small oligotrophic lake was artificially fertilized with phosphorus and nitrogen in an N:P ratio of 15:1 by weight from 1969 to 1974 (Schindler et al. 1971, 1973; Schindler and Fee 1974; Schindler 1975, 1977; Cruikshank 1984). Although phytoplankton primary production and standing biomass in Lake 227 were markedly enhanced following fertilization (Schindler et al. 1971, 1973; Schindler 1975), mean ice-free season biomass of many species of planktonic crustaceans and total biomass of rotifers in this low-carbon lake declined unexpectedly. Malley and Chang (1980) hypothesized that this was the result of loss of oxygenated, near-neutral pH habitat within the water column as a result of the fertilization.

One purpose of this paper is to describe the responses of various species of rotifers to the eutrophication of Lake 227. Mean ice-free season abundances of the crustacean species are described in Malley and Chang (1980). The second is to examine the time course of the changes in populations of both crustaceans and rotifers in relation to other physical, chemical and biological changes in the lake in order to test the above hypothesis and two others which may explain the zooplankton responses. The three hypotheses are:

1. The addition of fertilizer produced intolerable changes in the chemical environment, as proposed by Malley and Chang (1980).
2. The quantity of edible algal food for the zooplankton declined with fertilization.
3. Predation pressure due to fish or insect predators changed with fertilization.

MATERIAL AND METHODS

STUDY LAKE, FERTILIZATION PROCEDURE AND LIMNOLOGICAL SAMPLING

Lake 227 is situated in the Experimental Lakes Area (ELA) at 49° 42'N and 93° 42' W (Cleugh and Hauser 1971). The lake is 5.0 hectares in area, roughly circular in outline, with a mean depth of 4.4 m and a maximum depth of 10.0 m in the centre of the lake. Volume is 2.2 x 10^5 m^3. The enrichment procedure, water chemistry, primary production and phytoplankton are described by Schindler et al. (1971, 1973) and Findlay and Kling (1975). Fertilization began on 26 June 1969 with N:P added in a 15:1 ratio (molar ratio of 33:1). A total of 5.04 g N m^{-2} and 0.34 g P m^{-2} were added in 17 equal weekly additions in 1969, compared with estimated natural annual inputs of 0.53 g N m^{-2} and 0.02 g P m^{-2}. From 1970 to 1974 total annual experimental additions were 6.29 g N m^{-2} and 0.48 g P m^{-2} divided into 20 equal weekly additions between mid-May and mid-October.

ZOOPLANKTON SAMPLING AND ANALYSIS

Zooplankton were sampled using a transparent trap (Schindler 1969) of 28.7 L volume. Samples were taken once every two weeks to once per month starting on 17 May 1969. Sampling was carried on year-round until October 1971, following which zooplankton was sampled only during the ice-free seasons. Sampling was performed during daylight hours, usually in mid to late morning. Samples were taken in a vertical series at 1 or 2 m depth intervals at a single site in the lake, the point of maximum depth. As the trap was removed from the water, zooplankton were retained on a 53 µm mesh net. Samples from the epilimnion, metalimnion and hypolimnion were each separately pooled during periods of thermal stratification. Otherwise the entire vertical series was pooled. During 1969 to 1972, the entire water column (0 to 10 m) was sampled. In 1973 and 1974 zooplankton were typically sampled only down to a depth of 6 m (Chang et al. 1980). Each sample was preserved immediately with 4% formalin.

Identification and counting procedures are described by Chang et al. (1980). A total of about 55 zooplankton species was found in Lake 227 from 1969 to 1974, a number of which were rare. A complete species list and abundance of each species (numbers m^{-3}), except the rare, in each thermal layer, were reported by Chang et al. (1980). The six naupliar and six copepodid stages of copepods were separately reported. Also recorded there were epilimnion temperature, Secchi disc visibility and the actual depth strata sampled on each date.

Number of organisms of a species in a volume-weighted column of water under 1 m^2 of lake surface was calculated as follows:

$$\frac{\text{No. } m^{-3} \text{ in thermal layer X vol. of that layer, } m^3}{\text{surface area of lake, } m^2}$$

For preparation of the figures, numbers of individuals were summed over the three thermal strata. If the sample represented the entire water column, the density of individuals was multiplied by the lake volume and divided by the lake surface area. Numbers m^{-2} were averaged across sampling dates during May to September to obtain mean ice-free season abundances.

Dry weight biomass was calculated for the various life stages of each species from length, width and thickness dimensions of specimens taken at random from preserved Lake 227 samples as described by Lawrence et al. (1987).

Species diversity was calculated using the Shannon index of general diversity (Odum 1971):

$$\bar{H} = -\sum \left(\frac{n_i}{N} \log_e \frac{n_i}{N} \right)$$

where N = total number of individuals m^{-2} on the average over the May to September period and n_i is the number m^{-2} of each species on the average over the same period. Diversity of crustaceans was based on numbers of all cladocerans regardless of size and on adults only of copepods.

SAMPLING OF *CHAOBORUS*

Chaoborus in the water column were obtained incidentally at the time of zooplankton sampling. Counts of *Chaoborus* were performed on the entire volumes of zooplankton samples. Identification to species was made following Saether (1972). Instar determinations were made from length of the head capsule.

RESULTS

TOTAL BIOMASS AND DIVERSITY OF ZOOPLANKTON

The maximum recorded biomass of zooplankton, the mean ice-free season biomass and the seasonal changes in biomass were relatively similar among the three years 1969 to 1971 (Fig. 1). Maximum biomass was 685.6, 649.6, and 600.9 $mg \cdot m^{-2}$, respectively for these three years. Mean ice-free season biomass was 393.3, 259.4 and 287.5 mg m^{-2}, respectively for 1969 to 1971. Zooplankton were not sampled in years prior to fertilization which began on 26 June 1969. It is therefore not known whether the biomass present in 1969 to 1971 represents a change from pre-fertilization quantities. In 1969 to 1971, biomass was highest in the late May to July period and lowest at some time during the late August to October period. From sampling performed over the 1969-70 and 1970-71 winters, winter biomass was found to be at levels intermediate between these peaks. In 1972, mean biomass was markedly lower at 131.9 mg m^{-2}, although the seasonal pattern was the same as in the previous years. Zooplankton biomass in 1973 and 1974 did not follow the seasonal pattern of the previous years and mean biomasses were the lowest of the six years, 60.9 and 61.1 $mg \cdot m^{-2}$, respectively. Thus, beginning in late May 1972, total zooplankton biomass in Lake 227 had markedly decreased from that of previous years.

Diversity of crustaceans calculated as the Shannon index of general diversity, $\bar{H}$, was relatively unaffected by the fertilization until 1972, after which it declined markedly until 1974 (Fig. 2). Diversity of rotifers declined with time until 1972, then increased in 1973 and 1974. Diversity of rotifers in 1974 was similar to that in 1969 (Fig. 2).

ROTIFERS

Keratella cochlearis and *Polyarthra vulgaris* most consistently dominated the rotifer community of Lake 227, nevertheless, *Anuraeopsis fissa* was the species which reached the maximum abundance of any zooplankton species in the lake during this period (Table 1, Fig. 3). The response of rotifers to fertilization varied with the species, but two generalizations can be made. Abundances of most species were higher in the second and third years of fertilization, 1970 and 1971, than during 1969. In 1974, the abundances of the most common species were reduced to below those of 1969. These generalizations are reflected in the total rotifer biomass over time (Fig. 4D).

Filinia longiseta (Family Testudinellidae) was a species of secondary numerical importance (Table 1). It was relatively abundant in the summer of 1970, but maximum recorded abundance of *F. longiseta* was in January 1971 at 2 950 000 m^{-2} (Fig. 3A).

Polyarthra vulgaris (Family Synchaetidae) followed the above generalizations with highest mean abundance during 1970 to 1973 and reduced relative abundance in 1974 (Table 1, Fig. 3B). *P. remata* showed a divergent response to fertilization with numbers increasing each year after 1969 (Fig. 3C). Highest mean abundance was in 1974 (Table 1).

Trichocera cylindrica (Family Trichocercidae) was a rare species in 1969 which became still less common thereafter (Table 1, Fig. 3D).

Asplanchna priodonta (Family Asplanchnidae) also followed the generalization of highest populations in 1970 and 1971 (Table 1). Peak abundance was recorded in the fall during 1970, 1971 and 1972 but the fall peak was not seen in 1969 (Fig. 3E). 1973 and 1974 were years of declining abundance.

Keratella cochlearis (Family Brachionidae) was the most abundant species overall in Lake 227 during 1969 to 1974 (Table 1).

During September 1970 numbers reached 28 000 000 m^{-2} or 24 times the 1969 summer maximum. Abundances were highest in 1970 and 1971 (Fig. 3F). Except for one sampling date in 1971, K. taurocephala was rare after 1969 (Fig. 3G). Keratella hiemalis was highest in mean abundance in 1970 and lowest in 1971 and 1972 (Table 1, Fig. 3H).

Kellicottia longispina (Family Brachionidae) was well-represented from 1969 to 1971, thereafter was rare (Table 1, Fig. 3I). K. bostoniensis, on the other hand, was not recorded in 1969 and 1970 (Table 1), but was well represented in 1971 and 1972 (Fig. 3J).

The rotifer species which fluctuated most in abundance was Anuraeopsis fissa (Family Brachionidae). It was not recorded in 1969 and 1970 but achieved the highest ice-free season mean biomass of any zooplankton species in Lake 227 in this period with the highest recorded abundance, at 35 204 000 m^{-2} in 1971 (Table 1). During 1972 to 1974 mean abundances were considerably lower (Fig. 3K).

CLADOCERANS

Cladocerans in Lake 227 were represented by seven species, four of which were numerically important (Chang et al. 1980). Mean ice-free season abundances of cladocerans are reported in Malley and Chang (1980). Seasonal fluctuations in numbers were relatively similar between the years 1969 to 1970 for each of the four important species (Fig. 5A-D). Each species showed mid-summer blooms and very low overwintering abundances. The summer blooms did not develop in 1972 to 1974 or were much reduced with the exception of Diaphanosoma birgei in 1974.

Maximum abundance of Bosmina longirostris was recorded prior to fertilization, at 226 000 individuals m^{-3} (Fig. 5A). Diaphanosoma birgei (see Appendix 1) was generally uncommon in Lake 227 with the exception of one sampling date in 1974 when it occurred at an abundance of 197 000 m^{-3} (Fig. 5B). Holopedium gibberum was not present in the subsamples at all in 1972 and 1973 and was obtained on only one sampling date in 1974 at 1 700 m^{-3} (Fig. 5C). Like B. longirostris, Daphnia retrocurva was well-represented in 1969, 1970 and 1971, at lowest abundances during 1972 and 1973 and showed slight recovery of numbers in 1974 (Fig. 5D).

Cladoceran biomass showed a reproducible seasonal pattern in the years 1969 to 1971 but beginning in May 1972 failed to show the spring population increases (Fig. 4A). The otherwise lower biomass in 1974 was dominated by the high density of D. birgei on a single sampling date.

CALANOID COPEPODS

Mean ice-free abundances of calanoids are given by Malley and Chang (1980). If all life stages are included, Diaptomus minutus initially was the most abundant crustacean in Lake 227. Epischura lacustris was present in small numbers, and only in 1974. D. leptopus was recorded occasionally in the subsamples (Chang et al. 1980). Therefore, nauplii and copepodids were assumed to belong almost entirely to D. minutus.

In 1969 to 1970 D. minutus had an annual life cycle similar to that in Lake 132 (Schindler and Noven 1971). This species overwintered as adults (Fig. 6). Eggs were produced in late winter, reaching maximum numbers under the ice. Eggs hatched and development proceeded to naupliar stage 3 before ice-out. The maximum abundance of naupliar stage 4 occurred after ice-out. Most reproduction occurred by the end of May, but eggs were occasionally present until September.

Maximum naupliar abundance (stages 1 to 6 pooled) recorded in 1969 was 340 000 m^{-2} but peak numbers undoubtedly occurred in the weeks just before sampling began (Fig. 6A). Numbers of nauplii rose markedly in the early months of 1970. But the rise in numbers in early 1971 was much less. The abundance of nauplii obtained at the first sampling in May, 1972, was greatly reduced compared with that obtained during the same time period in 1969 and 1970. Between late July 1972 and 1974 numbers of nauplii were extremely low. The minor peak characteristic of July and August in 1969 to 1971 did not appear in 1972 to 1974. Copepodids, 1 to 5, primarily present from May to August/September, appeared to show a trend toward reduced numbers from 1969 to 1971 (Fig. 6B). They were present in only very low numbers in 1972 to 1974.

Adult D. minutus were most abundant in 1969, particularly in the first winter following fertilization (Fig. 6C). Numbers reached 122 000 m^{-2} in November, 1969. The mean May to September abundance in 1970 was substantially lower than in 1969 and few adults overwintered in 1970-71. Again in the ice-free season of 1971, abundance was lower than in 1969 and fewer adults were present in the fall than in 1970. During 1973 only a few D. minutus were obtained. Almost none were recorded in the subsamples in 1974. (Fig. 6c).

Examination of the 12 individual life stages indicates that abundances and seasonal distribution patterns of each life stage in 1970 were similar to those in 1969 up to copepodid stage 5 (Chang et al. 1980). Either these did not molt successfully to adults, or there was high adult mortality. The number of adults in the summer of 1970 fluctuated widely and by August was clearly below expected abundances. Ice-free season mean abundance was less than in 1969. Adults were scarce during the winter of 1970-71 (Fig. 6C). Nevertheless, those females that were present apparently reproduced normally. Egg : female ratios indicated no dramatic changes (Malley and Chang, unpubl. data). The development of naupliar stages was delayed in 1971, and there was a high mortality between naupliar stage 6 and the first copepodid stage. Samples were not taken during the winter of 1971-72, but in the spring of 1972 there were few females and few eggs. Few of the individuals hatching developed beyond naupliar stage 3.

Biomass of calanoids was highest in 1969 and 1970 and extremely low by late July 1972. Biomass remained very low through 1974 (Fig. 4B).

CYCLOPOID COPEPODS

Mean abundances of cyclopoid species and life stages are reported by Malley and Chang (1980). Lake 227 contained five species of cyclopoids, two of which, Cyclops vernalis and Orthocyclops modestus, were rare. Cyclopoid nauplii, not identified to species, were much less affected by the post-fertilization changes than were calanoids and cladocerans (Fig. 7A). Mean abundance was highest in 1970 and 1971, and less in 1969, 1972, 1973 and 1974. The copepodid stages 1 to 5 (Fig. 7B), also not identified to species, appear to have been reduced in numbers to a greater extent in 1972 to 1974 than the cyclopoid nauplii but not as dramatically as were the calanoids and cladocerans. Mean abundance was highest in 1969 and 1971, and consistently lower in 1970, 1972, 1973 and 1974. In 1972 and 1973 nauplii and copepodids were at low abundance in July and August unlike the three previous years.

Adults of Mesocyclops edax were more abundant in the summer of 1969 than during the subsequent five years (Fig. 7C). After 1969, this species was present sporadically and in low numbers. It was collected on only one date in 1972, not at all in 1973, and abundance in 1974 was similar to that in 1970 and 1971. Adults of Tropocyclops prasinus mexicanus had similar mean ice-free season abundances in 1969 and 1970. This species was not recorded in the subsamples during 1971 through 1974 (Fig. 7D). Cyclops bicuspidatus thomasi adults were obtained sporadically and in low numbers in 1969 and in 1970. In late 1970 and during 1971, the population was at its highest for this 6 year period. Numbers in 1972 and 1973 were as low as in 1969. The species was not recorded in 1974 (Fig. 7E).

Based on the 1969-1971 period, only one of the three cyclopoid species appeared to be dominant at any one period. For example, in midsummer of 1969, M. edax adults were abundant, the other two species were rare; in 1970 T. prasinus mex. dominated during mid-summer, and in 1971 C. bicuspidatus was abundant while the other two species were rare. Cyclopoids as a group demonstrated the most constant year to year biomasses of the crustaceans (Fig. 4C).

PHYSICAL FACTORS

Epilimnetic temperatures in the summers of 1969 and 1970 were similar and typical for ELA (Schindler 1971; Schindler et al. 1973). In 1971 and 1972 epilimnetic temperatures were about 2°C cooler (Schindler et al. 1973). Midsummer temperatures in 1973 resembled those of 1969 whereas the summer of 1974 was cooler and resembled 1972 (Chang et al. 1980).

CHEMICAL FACTORS

The low endogenous dissolved inorganic carbon (DIC) concentration for which Lake 227 was selected as an experimental lake, rendered it prone to pH changes (Schindler et al. 1971, 1973; Malley and Chang 1980). Prior to fertilization in 1969, the midsummer DIC concentration was about 50 µmoles L^{-1} and the pH was 6.5 to 7.2. Following the start of fertilization on June 26, increased rates of photosynthesis initially depleted these already low levels of DIC in the epilimnion. The lowest DIC values recorded in 1969 were about 10 µmoles L^{-1} on August 3, coinciding with the maximum recorded value of pH for that year of 9.4 (Table 2). Increase in pH is produced by exchange by the algae of NO_3 added as fertilizer for OH^- (Schindler et al. 1985). High pH values extended from the surface down to the mid-metalimnion and remained high through mid-September 1969. In 1970, fertilization began in mid-May, and the pH was increased much earlier in the season than in 1969. From late June until early September pH values down to a depth of 3.0 m were between 9.5 and 10.0 (Fig. 13 in Schindler et al. 1973). In 1971, from early June to late July, pH of the epilimnion was between 9.0 and 10.0. A period of cool, cloudy weather in July and early August was associated with fluctuating pH values from 6.4 to 9.3. Epilimnion pH up to 10.0 occurred again in late summer (Fig. 13 in Schindler et al. 1973). In 1972, pH was above 9.0 from the end of May until late July. The extreme value recorded that year was 10.19 on July 11 (Fig. 8). Schindler and Fee (1973) reported that the pH in the epilimnion of Lake 227 in mid-summer of 1972 changed only 0.1 to 0.2 pH units over the diurnal cycle. In 1973, epilimnion pH was between 9.0 and 10.0 from June until late July (Fig. 9). Epilimnion pH in 1974 was above 9.0 for several periods between mid-June and mid-September (Fig. 9).

The upper limit of the anoxic zone in midsummer, 1969, was generally deeper than 7 m (Fig. 2 in Schindler et al. 1971). The anoxic zone markedly thickened in the next two years and the upper limit rose to about 5.0 m in 1972 (Table 2). Consistent with this was a general decrease in the average summer oxygen content in the hypolimnion and the lower metalimnion of the lake from 1970 to 1972 (Table 2, Fig. 10, Schindler et al. 1973). The most extreme conditions were observed on July 11, 1972 (Fig. 8). On this date, the layer from 0 to 2 m was fully oxygenated, but O_2 concentration dropped sharply to 2 mg L^{-1} by 3 m depth. The lake winter-killed between 1973 and 1974 and the total water column was anoxic under the ice in April 1974 (Fig. 10).

Concentrations of ammonia, here including both NH_4^+ and NH_3, increased in the hypolimnion following fertilization due to the decay of phytoplankton (Schindler et al. 1971, 1973). The highest concentrations (>1000 µg L^{-1}) were associated with pH values below 6.5 (Fig. 8). At these pH values ammonia is present overwhelmingly as NH_4^+, the form relatively non-toxic to

fish and other aquatic organisms (Willingham 1976). Above pH 9.4 more than half of any ammonia present is in the toxic, unionized form, NH_3. Significant amounts of highly toxic undissociated NH_4OH can also be present. Nevertheless, concentration of ammonia in the alkaline epilimnion of Lake 227 with pH frequently above 9.4 was generally less than 10 ug L^{-1}. The maximum ice-free season ammonia concentration observed in 1969 to 1974 above the hypolimnion was 296 ug L^{-1} at a depth of 3 m, but at the pH of 6.8 little of this would be present as NH_3.

AVOIDANCE OF HIGH pH BY TWO CRUSTACEAN SPECIES

Adults and copepodids of Diaptomus minutus tended to be absent from the epilimnion of Lake 227 during periods of high pH. Fig. 11 indicates that a high proportion (50 - 100%) of the adults present in the water column of lakes 227, 302 South and 224 were in the epilimnion when the pH was near neutral. Lakes 302S and 224 were control ELA basins not subject to fertilization. The pH of the epilimnia of these was between 6.5 and 7.0. The pH of 9.0 to 9.3 in Lake 227 was usually associated with less than 50% of the individuals in the epilimnion. Most frequently, when the pH was above 9.5, D. minutus was absent from the epilimnion (Fig. 11). The absence may have been due to avoidance of the epilimnion by the copepods or to mortality in those individuals subject to the high pH or to both. In 1972 the extremely few, perhaps resistant, individuals present in the column were in the epilimnion in spite of pH between 9.5 and 10.1. Per cent of the population in the epilimnion in 1969 and 1970 was highly correlated with H^+ concentration ($r = 0.62$; $P<0.001$).

Like D. minutus, Bosmina longirostris was present predominantly in the epilimnion when pH was near neutral. This species appeared to avoid high pH less strongly than D. minutus, requiring a pH above 9.5 before it avoided the epilimnion (Fig. 11).

ALGAL FOOD SUPPLY

Phytoplankton standing crop increased several-fold in the weeks after fertilization began in June 1969. Estimated pre-fertilization mid-summer live biomass in the euphotic zone in 1968 was 1 000 $mg \cdot m^{-3}$, whereas in late August 1969 a maximum biomass of 4 800 $mg \cdot m^{-3}$ was reached (Findlay and Kling 1975). Species composition changes with fertilization are described by Schindler et al. 1971, 1973. In 1970, average mid-summer biomass was 6 000 to 10 000 $mg \cdot m^{-3}$, and maximum biomass, in late August was 15 000 mg m^{-3}. In 1971 standing biomass was somewhat below that of 1970, probably due to unusually cool August weather and biomass peaked at 7 600 mg m^{-3} in mid-July. In 1972 standing biomass increased further and on 26 July the maximum standing biomass of the 1969 to 1974 period was recorded at 63 000 mg m^{-3}. 1973 exhibited maximum biomass of 22 300 mg m^{-3} in early July (Findlay and Kling 1975). In 1974, biomass peaked at 12 000 mg m-3 (Findlay 1978). In all years algal cells of edible size, 20 µm and less, were abundantly available (Fig. 12). Phytoplankton was abundant down to a depth of more than 6 m during the summer (Schindler et al. 1973). The years of hignest biomass of edible phytoplankton, 1972 to 1974, were associated with lowest zooplankton biomass (Fig. 1, 12).

CHAOBORUS

Two species of phantom midge, Chaoborus flavicans and C. puntipennis were identified from the zooplankton samples taken during 1970 to 1974 (Fig. 13). Both species were most numerous in hypolimnion samples. Of the individuals counted in 1970 samples, 84% were in the lower layer samples (below 4 or 5 m depth), 9.5% in the middle layer samples (about 2 to 5 m depth) and 6.5% in the upper layer samples (surface to 2 m depth).

Individuals of the third instar were most numerous in the samples over the five years whereas individuals of the first instar were the least abundant. Although the samples from 1969 were not available for comparison, there is no suggestion of an increase in numbers from 1970 to 1972. Numbers in 1972, the year of most pronounced decline in zooplankton, were not higher than in other years. Low numbers in 1973 reflect the fact that depths below 6 m were not sampled. In 1974 depths below 6 m also were not sampled but substantial numbers were recorded from the middle depth layer. The high numbers of Chaoborus in 1974 follow the winter-kill period of April, 1974 which may have reduced fish predation on Chaoborus. An unusually high abundance of C. flavicans was recorded on August 13, 1974 (Fig. 13). Thus, numbers appear to have been substantially higher in 1974 than in other years.

FISH POPULATIONS

Although no long-term fish population studies have been carried out on Lake 227, several short-term studies have recorded the presence of minnows. In August, 1968, Libosvarsky (1968, unpublished MS) obtained no fish using gill nets of 2.5 to 9 cm mesh size but observed large schools of minnows near rocky shorelines. Gibbons (1971, unpublished MS), using gill nets and minnow traps in 1971 captured fathead minnows (Pimephales promelas), redbelly dace (Chrosomus eos), pearl dace (Semotilus margarita) and finescale dace (Chrosomus neogaeus). Using a mark-recapture method, he estimated that there were an average of 20 000 fishes in Lake 227 during July and August, probably an underestimate. Mills (Freshwater Institute, Winnipeg, Man. pers. comm.) captured no fish using gill nets in 1973. A further study during 23-25 August 1973, using gill nets of 2 cm mesh demonstrated that pearl dace were abundant and fathead minnows were rare (Beamish et al. 1976). Redbelly dace and finescale dace were not caught. In September 1979, Lake 227 contained large numbers of pearl dace, fathead minnows and a population of redbelly dace, finescale dace or a hybridization between them (K. Mills and S. Chalanchuk, pers. comm.).

Gibbons (1971, unpublished MS) found that the principal items in the diet of these minnows in 1971 were chironomid larvae, mayfly nymphs and algae. Zooplankton was a minor food item comprising less than 10% of the total food consumed (Table 3). Other work on these fish species from Lake 114 at ELA shows similar food composition (Tallman et al. 1984).

DISCUSSION

This paper shows that an increase in numbers and biomass of zooplankton in response to enhanced production and biomass of algae is by no means a general response to fertilization. In spite of the fact that the addition of nutrients to Lake 227 greatly increased the standing crop and production of edible phytoplankton, the process had a negative effect on total zooplankton biomass and crustacean abundance.

In an attempt to understand possible cause and effect relationships, co-occurrence between certain physical, chemical and biological changes in Lake 227 in response to fertilization and marked changes in zooplankton populations are examined. Each group of zooplankton responded somewhat differently to fertilization. The cladocerans showed little decline in numbers until the spring of 1972 when they failed to develop a spring bloom. The calanoids, represented principally by D. minutus, on the other hand, started to decline in 1970. The adults appeared to be the most sensitive life stage. Cyclopoids as a group responded the least to the fertilization but did exhibit lowered biomass in 1972 and 1973. Rotifers increased in numbers and biomass in 1970 to 1973 but particularly in the second and third years of fertilization, possibly in response to the decline of crustaceans. Nevertheless, they declined in abundance dramatically in 1974 in spite of little recovery of the crustaceans.

PHYSICAL ENVIRONMENT

Year to year or seasonal fluctuations in temperature were within the normal range for ELA and are not considered to be a causal factor in the zooplankton changes.

ALGAL FOOD SUPPLY

A marked increase in the quantity of algae of edible size or a shift of species to inedible forms in spite of an overall increase in total phytoplankton biomass could result in decline of zooplankton numbers. In the case of the eutrophication of Lake 227 during 1969 to 1974, neither of these situations materialized. There were ample quantitites of algae of edible size (Fig. 12) and the species present were edible (Findlay, pers. comm.). Thus the possibility that the zooplankton decline was related to insufficient food is rejected.

CHEMICAL ENVIRONMENT

Changes in the chemical environment following eutrophication are known to affect some zooplankton adversely (O'Brien and DeNoyelles 1972; Heisey and Porter 1977; Ravera 1980). The general inverse relationship between phytoplankton and zooplankton biomass in Lake 227 suggests the possibility that high algal biomass or productivity could have reduced zooplankton by causing intolerable changes in the chemical environment. Chemical changes may have resulted from a) high pH associated with removal of NO_3^- from the water by the algae, with the generation of alkalinity, b) removal of O_2 and production of toxic forms of ammonia by decomposition of enhanced algal biomass and c) production of toxins by algae.

Little information is available on the tolerance of zooplankton species to high pH. Lowndes (1952) reported that many species of Cyclops including C. bicuspidatus live in pH as high as 9.2. Davis and Ozburn (1969) reported that Daphnia pulex was able to withstand pH from 6.1 to 10.3 in river water (10 ppm of bicarbonate) but reproduction was observed only between pH 7.5 and 8.2. Field observations suggest that D. pulex survives from 5.8 to 9.2 (Lowndes 1952). O'Brien and DeNoyelles (1972) noted that high pH values of 10.5 to 11.0 in small ponds (75 ppm bicarbonate) receiving nutrient enrichment were associated with marked decrease and disappearance of crustacean zooplankton. Mid-morning pH values of 10.6 were associated with abrupt decline of numbers of Ceriodaphnia reticulata in the ponds and laboratory results suggested that a pH above 10.8 is acutely lethal to this species. Two species of cladocerans, Daphnia pulex and D. longispina and a cyclopoid, Thermocyclops oblongatus occurred in water of pH between 8.5 and to 10.1 in a South African lake (Connell 1978).

The maximum pH values recorded in Lake 227 were just over 10.0, considerably below the 10.8 suggested by O'Brien and DeNoyelles (1972) as acutely lethal to C. reticulata. Nevertheless, acutely lethal pH values for Lake 227 species are expected to be below those reported by O'Brien and DeNoyelles (1972) because of the softer water (about 3 ppm of bicarbonate in Lake 227). Also the Lake 227 species are lake rather than pond species, presumably adapted to more constant and moderate conditions.

Von Brand (1944) reported that several species of Cyclops could survive anoxic conditions. Adults of Cyclops varicans from an impoundment were shown to tolerate at least 36 h of anaerobic conditions by building up an oxygen debt (Chaston 1969). Mesocyclops edax has been found to survive several weeks of anoxia under winter ice (Schindler and Comita 1972). No freshwater calanoids are reported to tolerate anaerobic conditions.

Few data are available, and these are highly discrepant, on the concentrations of NH_3 which are toxic to zooplankton. One study suggests that no effect on zooplankton populations

occurs at concentrations less than 2500 µg L^{-1} (Grygierek et al. 1979). A chronic concentration of 20 µg L^{-1} NH_3 is deemed safe to fish by Willingham (1976) and nontoxic to other aquatic organisms (EIFAC 1973). Therefore, it seems improbable that the NH_3 concentrations in the epilimnion of Lake 227 at concentrations less than 10 µg L^{-1} were toxic to zooplankton.

Primary producers are known to produce toxins which affect zooplankton. Some of the algal species present in Lake 227 during the post-fertilization period are known to produce toxins under some circumstances, for example, Aphanizomenon flos-aquae and Scenedesmus quadricauda (Gentile, 1971). A toxic strain of A. flos-aquae was required at 1 x 10^6 cells mL^{-1} to kill Bosmina longirostris; at 4 x 10^7 cells mL^{-1} to kill Daphnia catawba; and at 1 x 10^8 cells mL^{-1} to kill cyclopoid copepods (Gentile 1971). At no time were these two phytoplankton species abundant enough in Lake 227 to produce lethal amounts of toxins even if they were toxin-producing strains.

We conclude that the most plausible cause of crustacean zooplankton decline in Lake 227 in 1970 to 1973 was high pH in the epilimnion and low O_2 in the metalimnion and hypolimnion. The high pH is the direct result of photosynthesis stimulated by fertilization. Increased algal production resulted in greater decomposition in the metalimnion and hypolimnion, causing low oxygen concentrations in these regions. Zooplankton were thus progressively "squeezed" over the years of fertilization between toxic pH values in the epilimnion and low O_2 in deeper strata. Not unexpectedly, calanoids were found to be more sensitive to these conditions than the cladocerans. Cyclopoid copepods were least affected presumably because of their greater tolerance to low O_2 and high pH.

PREDATION

It appears unlikely that the fish populations in Lake 227 preyed heavily enough on zooplankton to account for the observed decreases in abundance in the post-fertilization period even if the fish populations of the lake increased during the period. The response of zooplankton to intense predation by fish is usually a shift to smaller species (Brooks and Dodson 1965; Warshaw 1972) or to smaller-bodied individuals within a species such as Daphnia (Northcote and Clarotto 1975). There was no relation between body size and order of decline in population size for species in Lake 227. Intermediate-sized, adult D. minutus were the first crustaceans to decline in numbers. The largest crustaceans, M. edax, although most abundant in 1969, were as abundant in 1971 as in 1970, whereas the small T. prasinus mex., present in 1969 and 1970, were not recorded in 1971 to 1974. In 1972, small-bodied B. longirostris showed small populations as did the large species.

Invertebrate predators such as Cyclops bicuspidatus thomasi and Mesocyclops edax may play a role in reducing the standing stocks of nauplii and certain species of rotifers such as Asplanchna priodonta and Polyarthra vulgaris (McQueen 1968; Gilbert and Williamson 1978). Nevertheless, adults of these cyclopoids were not particularly abundant when the calanoids and cladocerans declined in abundance and they are not implicated in their declines. Lewis (1977) suggests an order of selectivity of prey by Chaoborus that is generally applicable to many different Chaoborus species and many different lakes:
Bosmina>copepod copepodids and adults>Diaphanosoma>rotifers>nauplii>Daphnia. If such selectivity is applicable to Lake 227, and if predation by Chaoborus were responsible for the decline of the crustacean populations it seems unlikely that all species of cladocerans would have declined in abundance at the same time, in 1972, as we observed.

Abundances of Chaoborus reported here in Lake 227 were much lower than those reported in other estimated here from the daytime zooplankton samples were seldom over 100 m^{-2} (Fig. 13). Considering that both these species of Chaoborus tend to be benthic by day (Roth 1968), sampling by zooplankton trap during the day almost certainly underestimated numbers. Nevertheless, if one assumes that zooplankton sampling each year from 1970 to 1972 captured roughly a constant proportion of the sample then there is a lack of relationship between apparent numbers of Chaoborus in 1970 to 1972 and the abrupt decline in crustacean numbers. Thus, it is unlikely that Chaoborus was responsible for the decline in crustaceans in 1971 and 1972.

In 1974, there was a significant increase in the number of Chaoborus captured by day in the water column (Fig. 13), particularly taking into account that the bottom waters, 6 to 10 m where most of the Chaoborus were found in 1970, were not sampled in 1974. In 1974, total zooplankton biomass remained low but the contributions by the various groups drastically changed. Rotifers dropped from 88% of zooplankton biomass in 1973 to 11% in 1974; Cladocera increased from 1% in 1973 to 51.5% in 1974. Yan et al. (1982) reported that Chaoborus in an acidic fishless lake increased dramatically upon fertilization. The Chaoborus appeared to prey heavily on rotifers and copepod nauplii. In Lake 227 in 1974 cladocerans were able to make some gains in abundance, particularly due to a bloom of D. leuchtenbergianum. Possibly cyclopoids would also have increased but were kept at low numbers because of intense predation by Chaoborus. Further, the decline in abundance of rotifers may have been the result of Chaoborus predation due to insufficient copepod prey.

TIME COURSE OF ENVIRONMENTAL CHANGES

Although Lake 227 was subjected to identical areal loadings of N and P in each of six years, apart from the slightly lower total amounts added in 1969, the responses of the zooplankton varied considerably between years.

Fertilization touched off a chain of biological and chemical events each with its own temporal response and subject to modification by year-to-year climatic variation. The standing

algal biomass achieved in 1969 was the lowest of the six years (Findlay and Kling 1975). Even so, the moderately high maximum pH of 9.4 may have been high enough to be toxic to some zooplankton species, but the metalimnion was available as a refuge with moderate pH and O_2 levels. In 1969 the average volume of the epilimnion available for dilution of the added nutrients was the largest of the six years (Table 4). In 1970, nutrient addition began five weeks earlier and the epilimnion volume in which nutrients were diluted was considerably smaller than in 1969. The earlier nutrient additions or higher nutrient concentration may have caused the higher standing algal biomasses of that year. The pH values achieved that year were correspondingly higher than in 1969 (Table 2). The decline in numbers of D. minutus is attributed to the toxic effects of high pH. 1970 was the only year of the six to show spring turnover of the water column. This may have retarded the deoxygenation of the water column resulting from the breakdown of the increased algal biomass. Lower standing algal biomass in 1971 is attributed to cool, cloudy weather but is also correlated with a large epilimnion volume as in 1969. 1971 showed lower maximum pH values than in 1970 and periods of return to near-neutral pH. The anaerobic zone in the lake was not thicker than in 1970 (Table 2). The calanoids continued not to tolerate the chemical conditions and were lower in abundance than in 1970. On the other hand, the cladocerans and cyclopoids showed no reduction in numbers. If 1971 was a year in which adverse trends were momentarily halted, in 1972 they resumed again. There was no spring overturn. At ice-out the 2 $mg \cdot L^{-1}$ O_2 isopleth was 2 m higher in depth than in 1971, algal biomass was higher in April than in previous years (Findlay and Kling 1975) and elevated pH levels occurred earlier in the spring than in previous years. Individuals of these factors or their combination are believed to be responsible for the failure of the four cladoceran species to show their spring bloom. The very low oxygen concentrations in the metalimnion reduced its importance as a refuge between the high pH, oxygenated epilimnion and the neutral, anoxic hypolimnion. The cyclopoids, more physiologically-tolerant than the calanoids and cladocerans, also showed reductions in abundance. The marked reduction in crustacean grazing pressure is correlated with exceedingly high phytoplankton biomass in July of 63 g m^{-3}. The year 1973 was similar to 1972 in epilimnion volume, chemical parameters and overall zooplankton responses. Schindler (1975) reported a gradual increase in the total amount of C in Lake 227 from 1969 to 1973. The CO_2 invaded from the atmosphere to supply C needs not met from the dissolved pool. The result was a sufficiently-elevated DIC pool by 1974 such that pH did not reach the extremes of other years. This was in spite of the smallest epilimnion volume of the six years. Cladocerans showed some signs of recovering their numbers but the winter-kill of April 1974 is believed to have favoured large populations of Chaoborus. The Chaoborus may have been responsible for reducing the abundances of rotifers and for keeping copepod abundances low.

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APPENDIX 1

Appendix 1.

Diaphanosoma in Lake 227 are identified as Diaphanosoma birgei. (Korinek 1981). This population has been called after D. brachyurlum in Chang et al. (1980), and Malley and Chang (1980). It is probably the D. leuchtenbergianum of other authors. There is considerable confusion in the exact relationships among D. birgei, D. leuchtenbergianum, and D. brachyurum as used by different authors.

Table 1. Number m^{-2} of rotifers in Lake 227 averaged over the May to September period during six years.

Species	1969	1970	1971	1972	1973	1974
Filinia longiseta	31 800	446 600	79 700	86 500	285 700	1 390
Polyarthra vulgaris	126 700	365 200	1 152 100	769 600	732 300	25 600
Polyarthra remata	8 300	22 600	52 200	21 000	34 200	133 900
Trichocerca cylindrica	6 000	1 500	550	250	280	290
Asplancha priodonta	23 800	28 000	73 400	27 900	19 200	2 600
Keratella taurocephala	23 500	200	9 300	4 300	1 000	2 100
Keratella cochlearis	342 500	2 307 000	3 811 900	4 454 600	1 803 600	14 300
Keratella hiemalis	13 100	258 600	2 800	1 100	94 100	63 100
Kelicottia longispina	170 200	231 200	31 500	1 500	2 300	2 300
Kellicottia bostoniensis	0	0	105 800	29 700	8 000	19 600
Anuraeopsis fissa	0	0	8 349 400	1 170 000	858 900	531 300

Table 2. Summary of mid-summer (July and August) O_2 and pH levels in Lake 227 for the years 1969 to 1974.

	1969	1970	1971	1972	1973	1974
Approximate depth of the upper limit of anoxic zone	7.0 m	6.0 m	6.0 m	5.0 m	5.0 m with 4.0 and 3.0 m on occasion	5.0 m
Estimated depth at which O_2 conc. is 2 $mg \cdot L^{-1}$	5.5-6.5 m	4.5-5.5 m	4.75 m	2.5-3.0 m	2.75 m (1.75-4.25 m range)	3.5 m
Maximum recorded pH in the epilimnion	9.40	10.21	9.90	10.19	10.01	9.77

Table 3. Stomach contents (percentage volume) of four species of fish from Lake 227 in 1971*.

Stomach contents	Pearl dace			Redbelly dace			Fathead minnow			Finescale dace		
	Jul 9	Jul 29	Aug 12	Jul 9	Jul 29	Aug 12	Jul 9	Jul 29	Aug 12	Jul 9	Jul 29	Aug 12
Phytoplankton	26	41	8	43	23	18	36	27	23	0	-	0
Zooplankton	3	2	0	5	6	15	8	6	9	0	-	0
Chironomid larvae	64	25	41	41	71	44	44	63	55	0	-	17
Mayfly nymphs	2	31	39	0	0	7	0	0	0	0	-	5
Terrestrial Diptera	5	1	12	11	0	14	12	4	13	100	-	78

* unpublished data, J. Gibbons (1981).

Table 4. Time-weighted average thickness and volume of epilimnion of Lake 227 between time of stratification (about day 123) and day 243 for the years 1969 to 1974.

Year	No. of determinations of thermal profile	Average thickness of epilimnion m	Average volume of epilimnion x 10^3 m^3
1969	9	2.07	84.7
1970	20	1.64	68.6
1971	18	2.23	89.0
1972	14	1.66	70.6
1973	9	1.69	71.6
1974	8	1.59	66.3

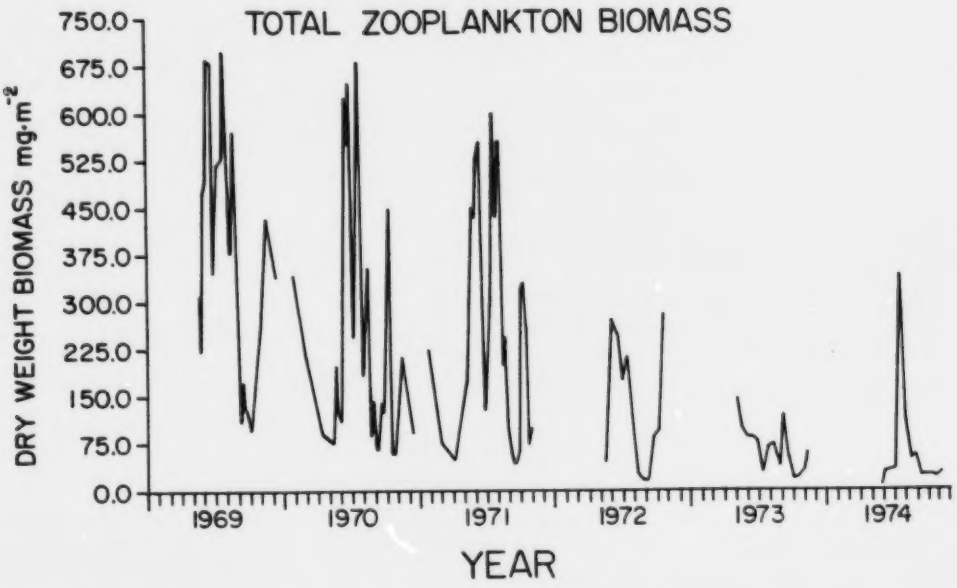

Figure 1. Total dry weight biomass in $mg \cdot m^{-2}$ of zooplankton in Lake 227 for 6 years.

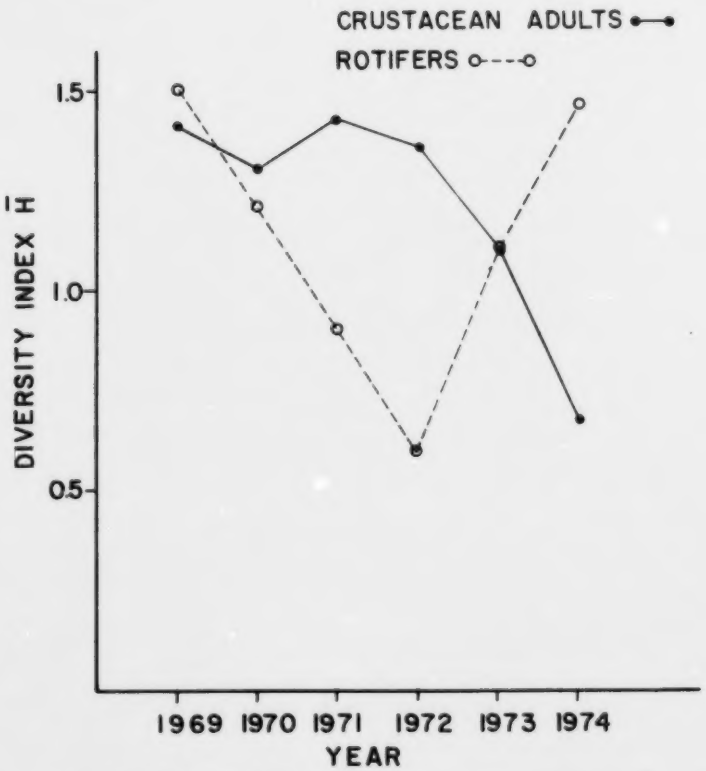

Figure 2. Change in Shannon index of general diversity, $\overline{H}$, with time for adult crustaceans and for rotifers in Lake 227 calculated from mean abundances of species during the May to September periods of 6 years.

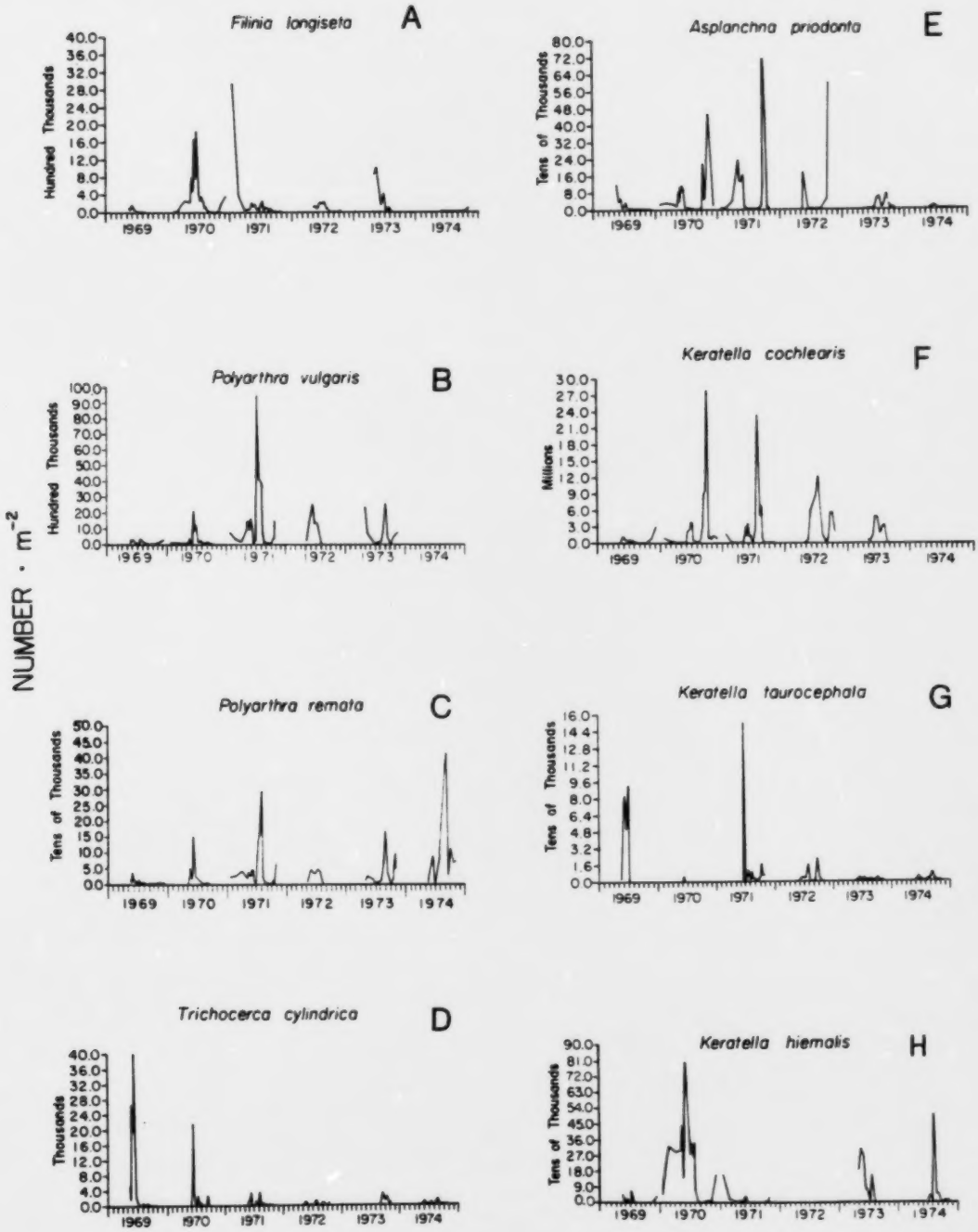

Figure 3. Number m^{-2} of each of eleven species of rotifers (A to K) in Lake 227 for 6 years.

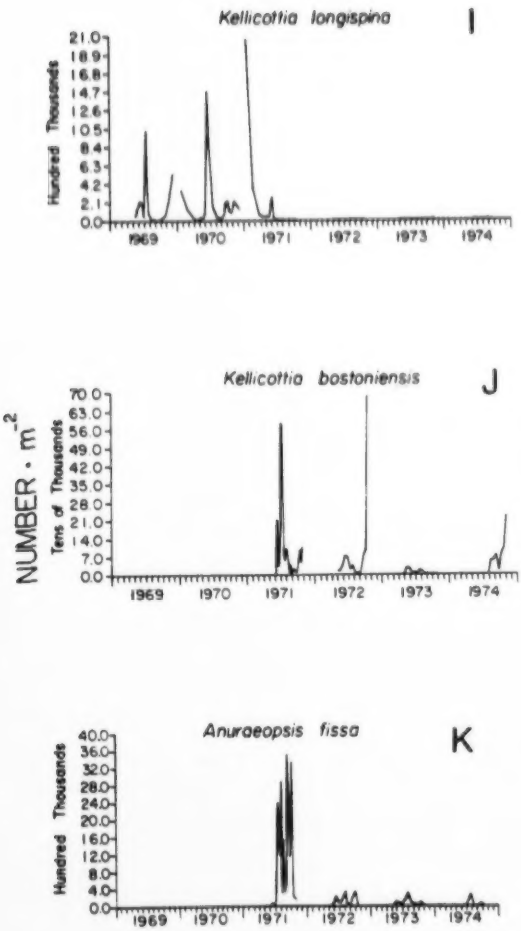

Figure 3. (cont'd.)

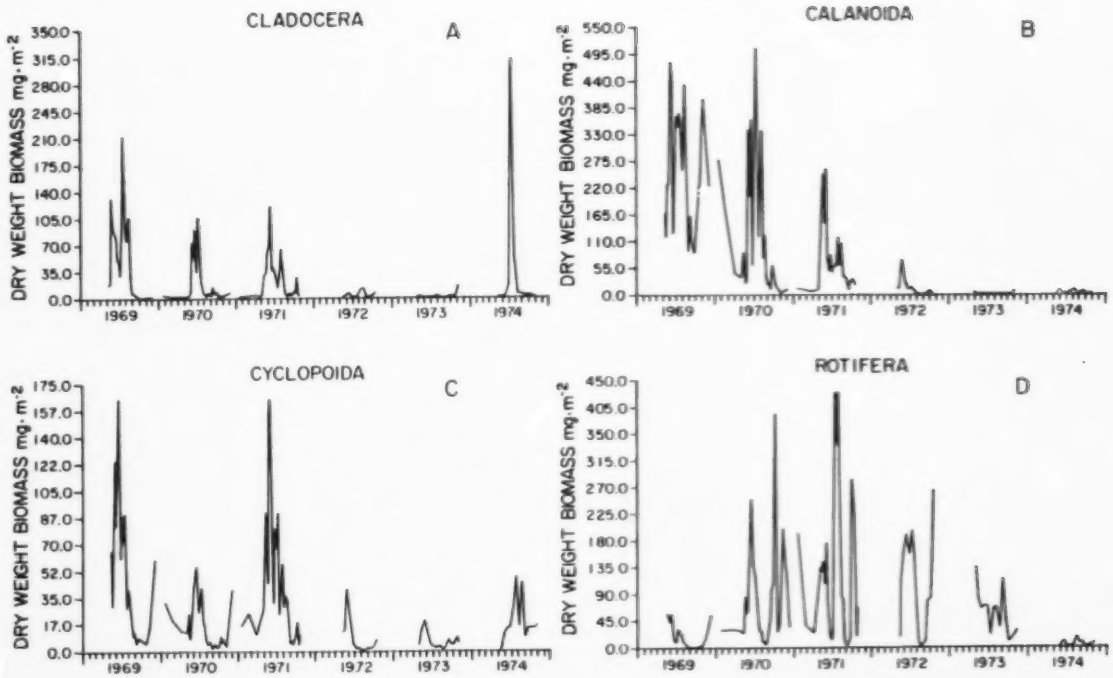

Figure 4. Total dry weight biomass in $mg \cdot m^{-2}$ of cladocerans (A), calanoids (B), cyclopoids (C) and rotifers (D) in Lake 227 for 6 years.

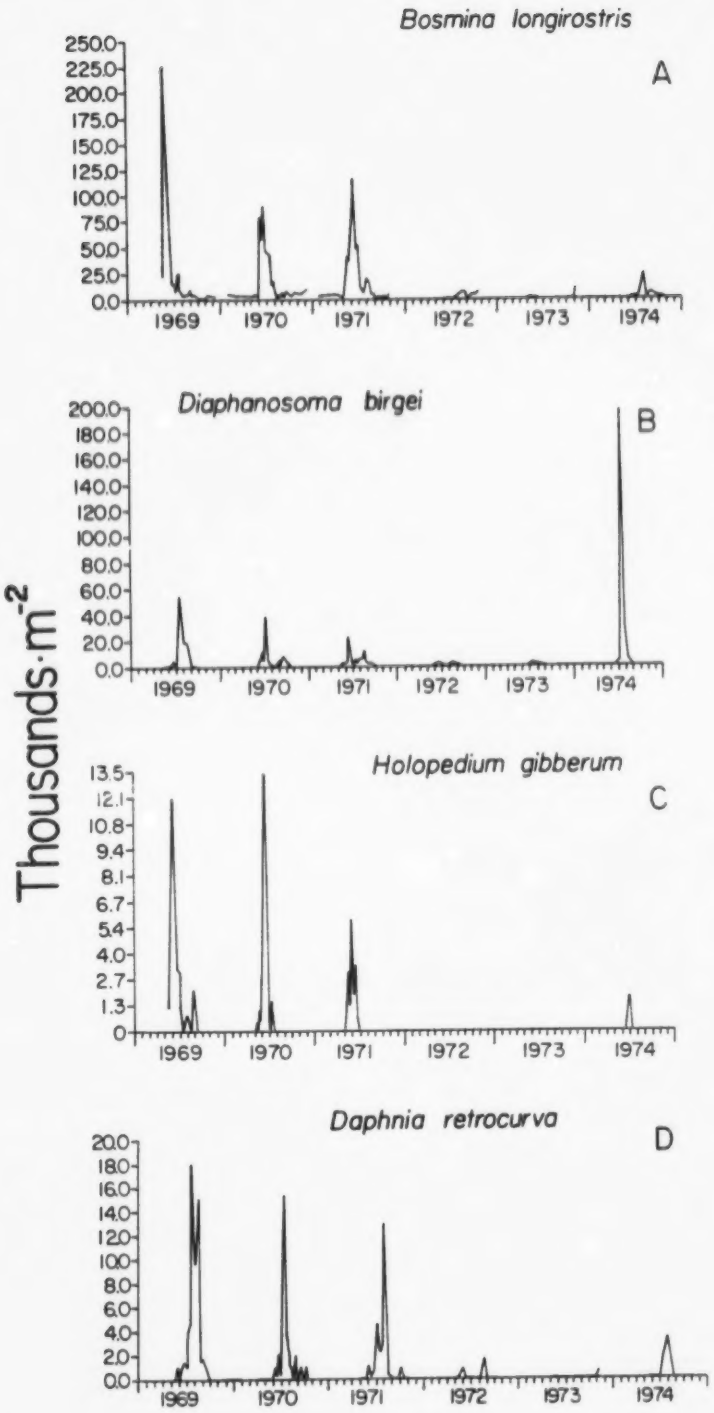

Figure 5. Number m^{-2} of all sizes of each of four species (A to D) of cladocerans in Lake 227 for 6 years.

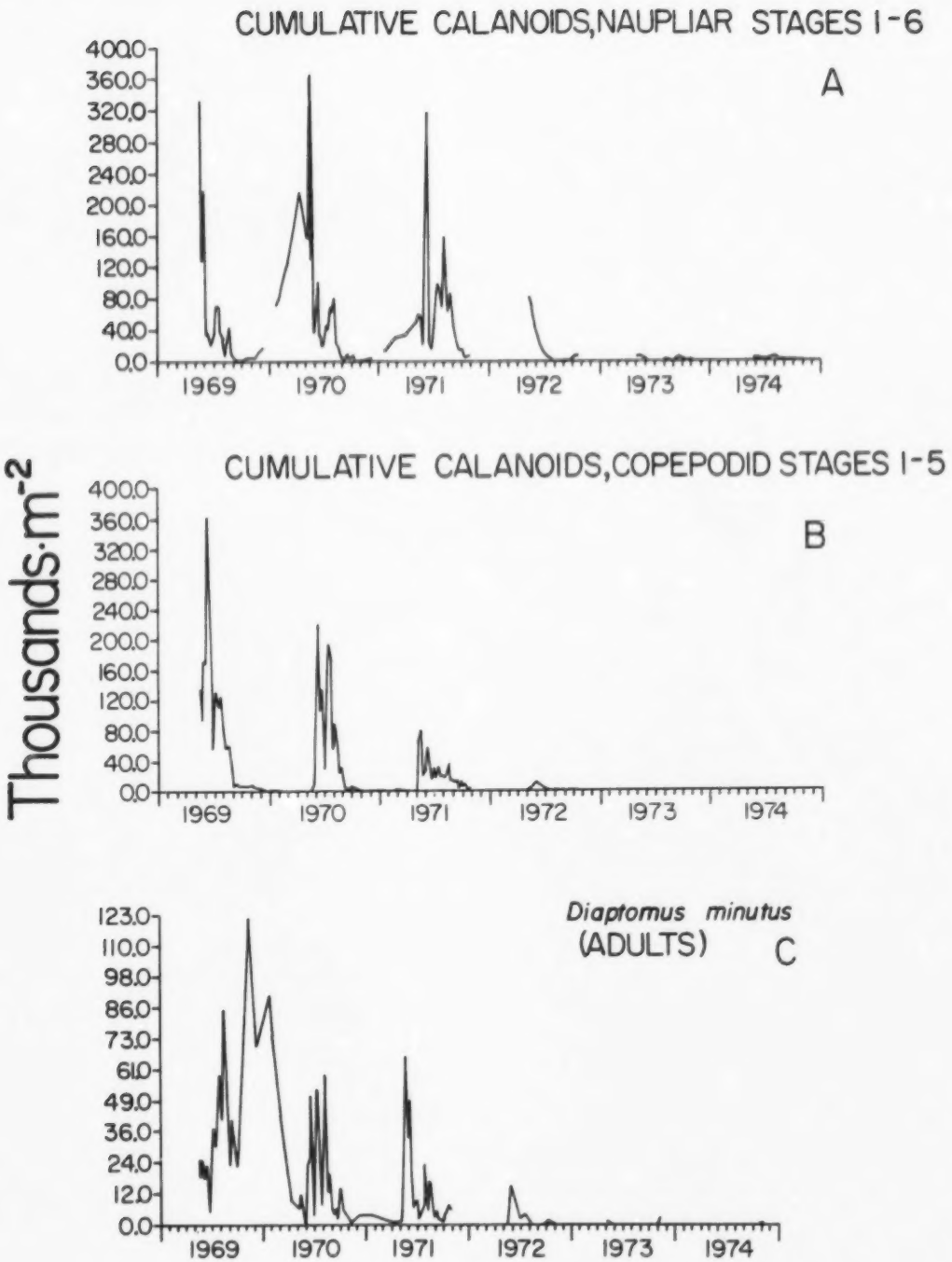

Figure 6. Number m^{-2} of calanoid copepods grouped as nauplii (A), copepodids 1 to 5 (B) and D. minutus adults (copepodid 6) (C) in Lake 227 for 6 years.

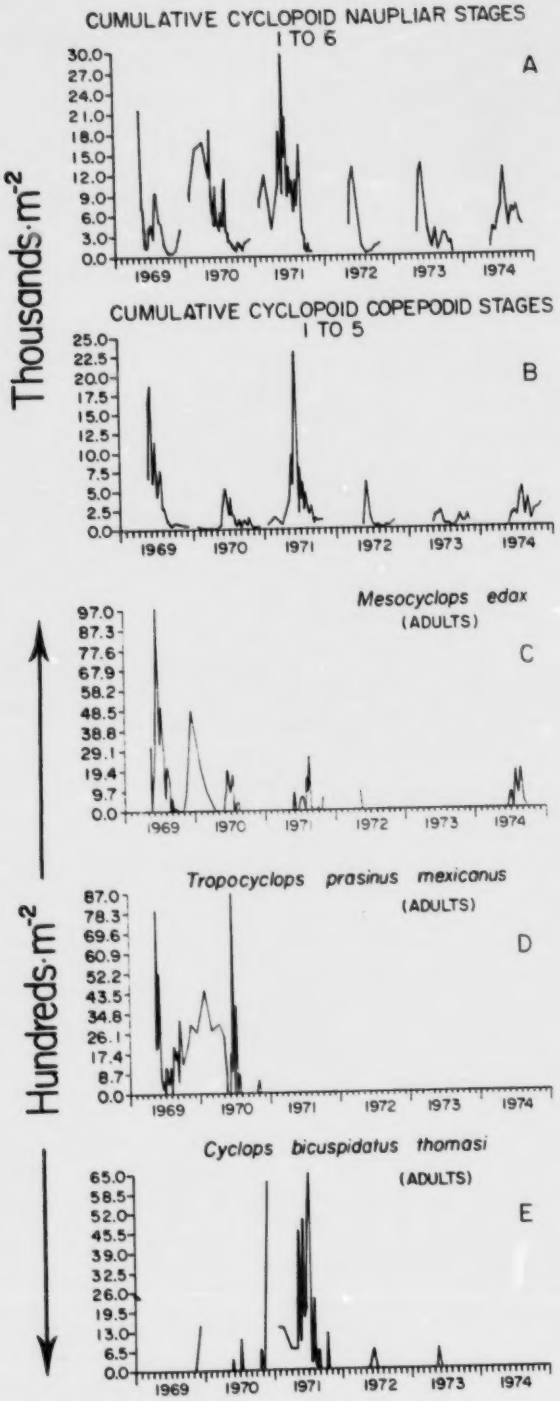

Figure 7. Number m^{-2} of three species of cyclopoid copepods in Lake 227 for 6 years. Nauplii (A) and copepodids 1 to 5 (B) are pooled over the three species. Adults of the three species are shown in C, D, E.

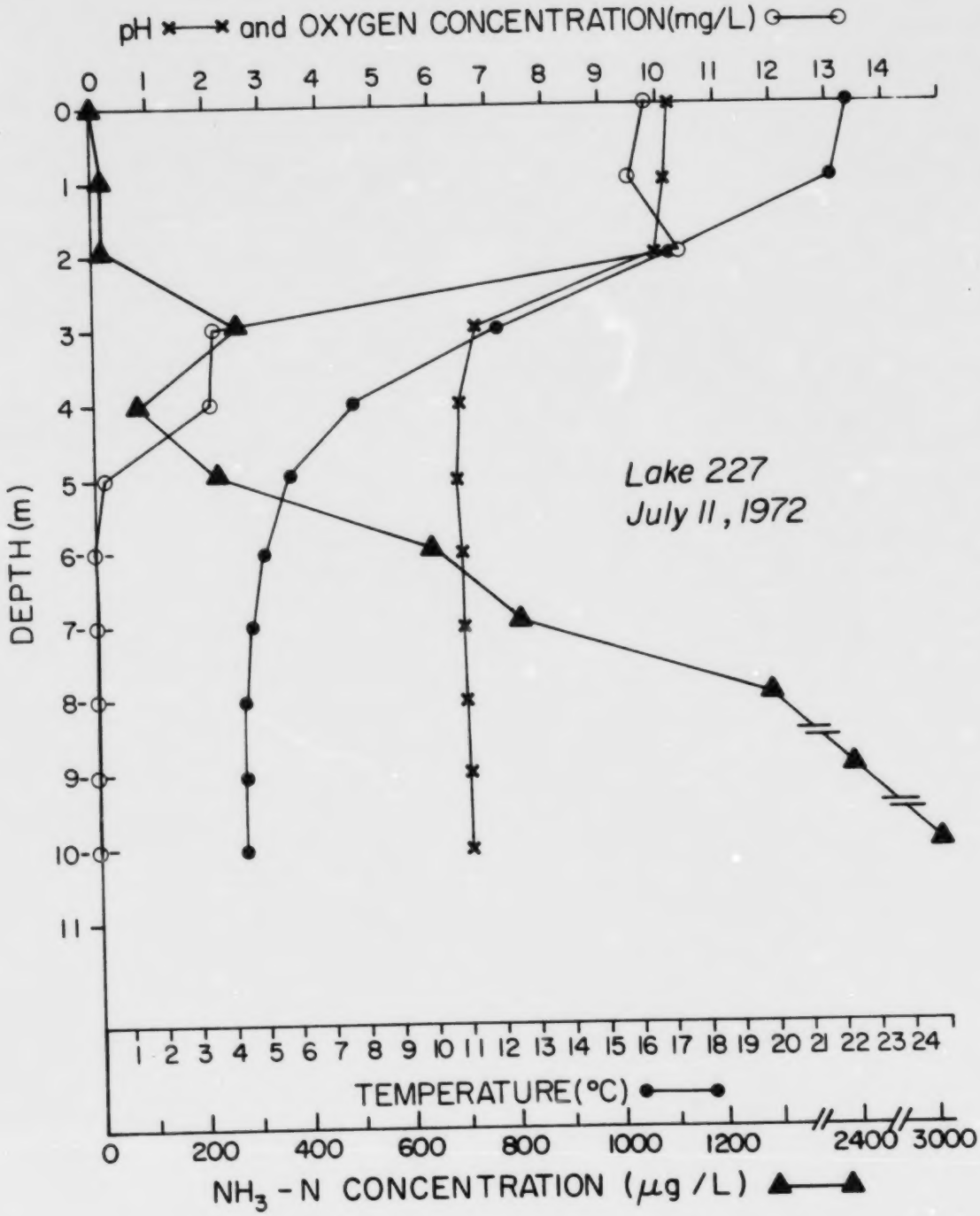

Figure 8. pH, oxygen, temperature and ammonia profiles in Lake 227 on one post-fertilization date, 11 July 1972.

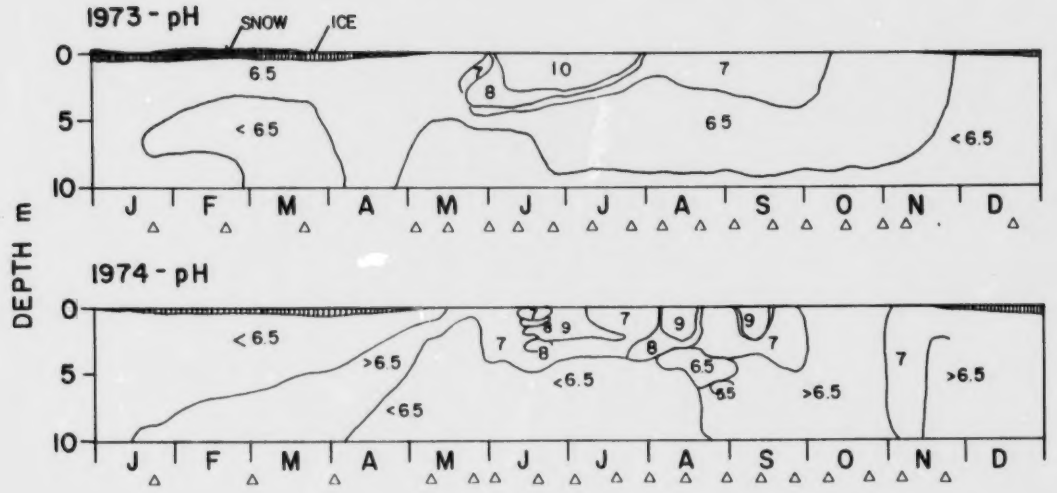

Figure 9 Seasonal isopleths of pH for 1973 and 1974. Data for earlier years are given by Schindler et al. (1971, 1973).

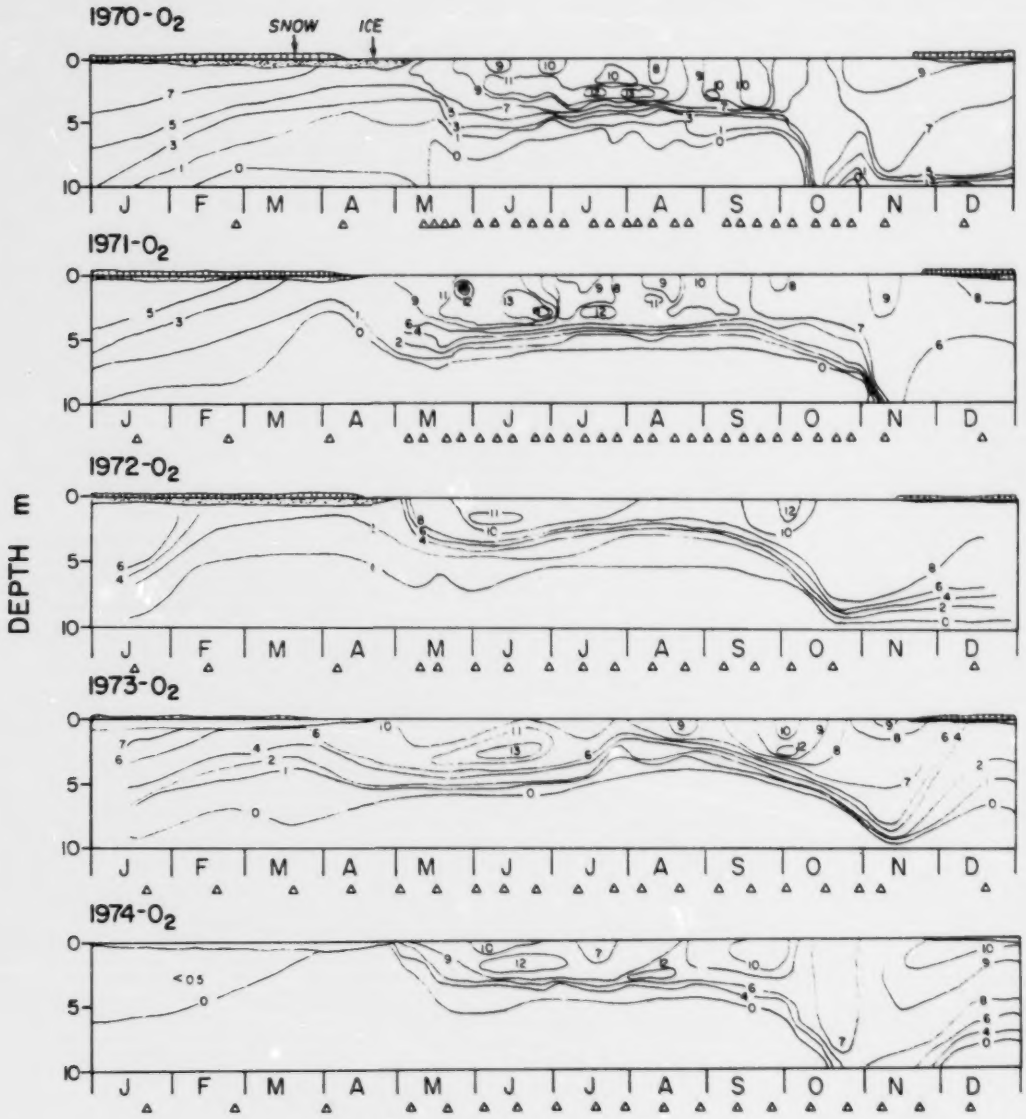

Figure 10. Seasonal isopleths of O_2, mg L^{-1}, for 1970 to 1974. Data for 1969 are given by Schindler et al. (1971).

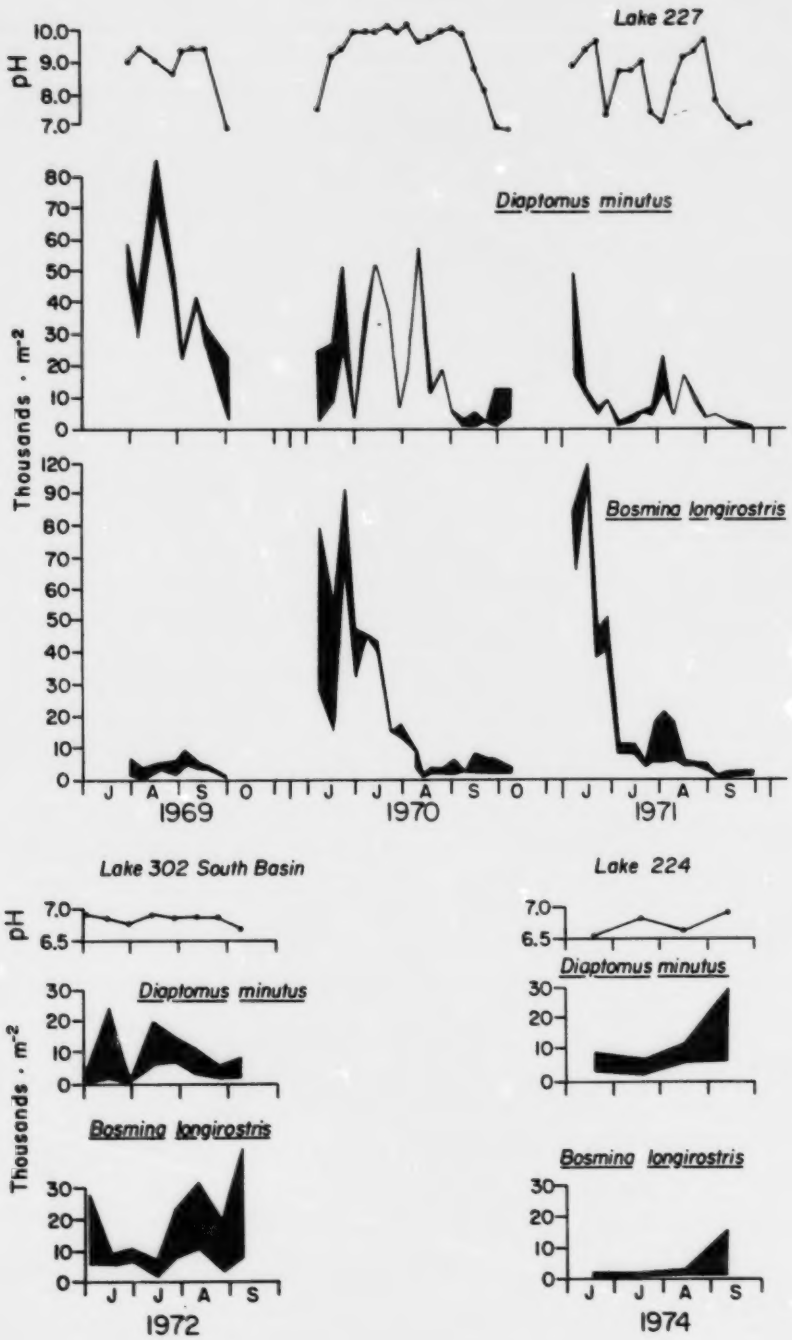

Figure 11. Abundances of Diaptomus minutus (adults) and Bosmina longirostris in the epilimnion (black area) and below the epilimnion (white area below black) of Lake 227 (upper half of figure), Lake 302 south basin (lower left) and Lake 224 (lower right). pH of the epilimnion is given for the same periods in each lake.

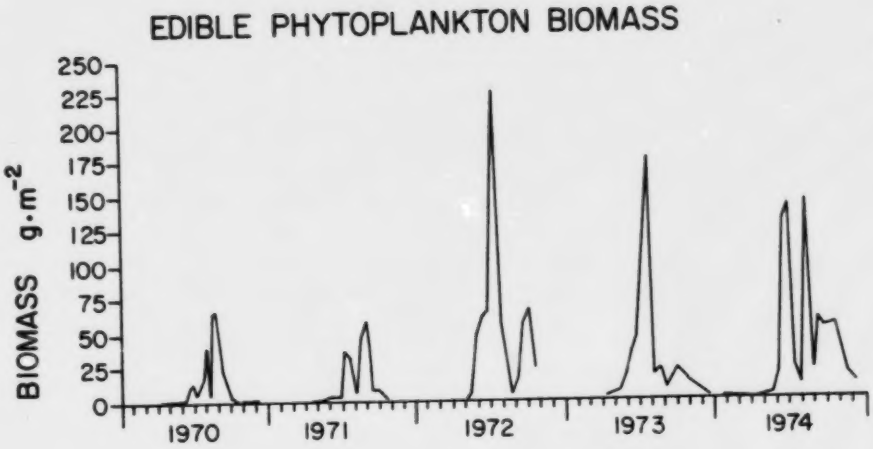

Figure 12. Total live biomass in $g \cdot m^{-2}$ of phytoplankton of edible size in Lake 227 for 5 years. Edible algae were defined as those <20 µm in all dimensions and excluded those in chains or with spines. (Data supplied by D.L. Findlay and S. Kasian).

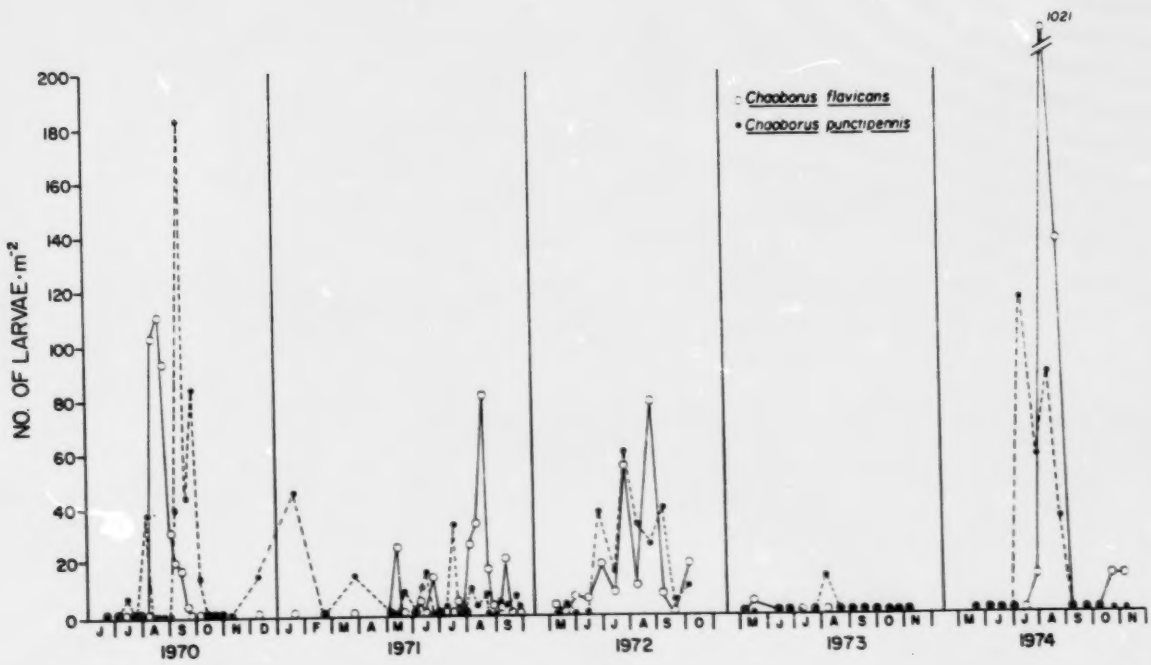

Figure 13. Number m^{-2} of two species of Chaoborus obtained during daytime sampling for zooplankton in Lake 227. Six to nine months of data are shown for each of 5 years. In 1973 and 1974 only 0 - 6 m depths were sampled.